OBSERVATIONS ON THE EGG-CASES OF SOME OVO-VIVIPAROUS AND VIVIPAROUS ELASMOBRANCHS, WITH A NOTE ON THE FORMATION OF THE ELASMOBRANCH EGG-CASE[1]

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(*With a plate*)

INTRODUCTION

Egg-cases of a number of oviparous Elasmobranchs have been described from time to time, the oblong egg-capsules of skates and rays being known as 'skate barrows,' 'sailors' purses,' 'mermaids' purses,' and 'mermaids' pin-boxes'. As in all the oviparous species known so far, so also in all ovo-viviparous and most of the viviparous species, the egg is protected by an egg-case. But little attention seems to have been paid to the study of the egg-cases of ovo-viviparous and viviparous Elasmobranchs.

Prasad (1945 a, b and 1948) reported certain structural modifications that had been observed in the nidamental glands of Elasmobranchs as oviparity gives place to viviparity. In a recent paper Matthews (1950), while describing the nidamental glands of *Cetorhinus maximus* remarks: 'The structure of the gland in *Cetorhinus* is such as to suggest that its function is solely that of secreting albumen; if any shell is produced it is unlikely to be more than a membranous sac, as in *Acanthias*'. The present work was started with a view to study the probable changes that might result in size, shape and structure of the egg-cases of ovo-viviparous and viviparous Elasmobranchs as oviparity gives place to viviparity and the following is a preliminary report on the observations made on a few ovo-viviparous and viviparous Elasmobranchs of the Madras Coast.

EGG-CASES

The best developed egg-capsules are naturally those of oviparous forms. They vary from the simple horny capsules of many of the common oviparous species to the highly developed egg-capsule of *Heterodontus*, where it is of relatively large size and has the form of an elongated conical capsule with very thick walls, provided with two broad flat flanges twisted spirally around it and two long coiled filaments at the pointed end. Variations in the egg-cases are found

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[1] This investigation was carried out while the author was working in the Madras University Zoological Research Laboratory, but the publication has been delayed owing to his being away on an Overseas Scholarship.

even within the same family. Such differences are given by Clark (1922) who has described the egg-capsules of eight species belonging to the family Raiidae. He mentions also that capsules spawned by the same fish show considerable variation in size. In the egg-cases of some of the oviparous species the four corners are drawn out into long tendrils; in some others the four corners may be produced into horns of varying lengths; in some only two corners are produced into long horns, the other two being short, stumpy and strongly hooked; in still others there are numerous delicate filaments on the two side margins of the egg-case. The tendrils, horns and filaments are all considered to be different aids for anchoring the egg-capsule. Of the egg-cases belonging to the different species of oviparous Elasmobranchs, the largest recorded is one hundred and eighty millimeters in length and about one hundred and fifty millimeters in width, the smallest about sixty-three millimeters in length and thirty-seven millimeters in width (Norman, 1947). Among the egg-cases of the various species of the family Scyllidae, Smedley (1926) observed a gradation. He says: 'The members of the family Scyllidae inhabiting Malayasian waters provide examples of three distinct types of egg-cases. 'That of the genus *Scyllium* has the four corners produced to form long tendrils, and it is not until these have become firmly entwined around some fixed object that the egg-case is drawn from the oviduct of the female. *Chiloscyllium indicum* has a band of fine mucilaginous hairs which may form a means of anchorage after the laying of the egg. 'In the case of *Stegostoma* no method of attachment is provided and the egg apparently drifts until the hatching out of the young shark.'

These are typically oviparous forms. The next stage in the gradual transition from oviparity to viviparity is the ovo-viviparous condition. Since in the ovo-viviparous and viviparous forms the egg-case is retained in the uterus the means of anchorage such as tendrils and mucilaginous hairs have been lost. Probably egg-cases such as those of *Stegostoma* indicate the transitional stage through which Elasmobranchs passed gradually from oviparity to ovo-viviparity[1].

The egg-case of *Chiloscyllium griseum*, an oviparous species, found commonly along the Indian Coast, has been described by Aiyar and Nalini (1938) and Nalini (1940).

Of the ovo-viviparous Elasmobranchs that occur along the Madras Coast, the author has examined the egg-cases of *Rhinobatus granulatus*, *Rhynchobatus djiddensis* and *Pristis cuspidatus*. All these have almost similar egg-cases measuring on an average 250 mm. by 120 mm. Each egg-case is a large bag made up of two lateral halves,

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[1] The term ovo-viviparity is here used to include those cases in which the eggs, enclosed in an egg-case, are retained in the uterus until the young ones hatch by rupturing the egg-case. There is neither a placenta formed nor is there a direct feeding mechanism by the trophonemata of the maternal uterine wall. The term viviparity, on the other hand, is used to include those cases in which the eggs undergo development in the uterus and the young ones hatch and usually there is the formation of the yolk-sac placenta or the maternal uterine villi or the trophonemata pour their secretion directly into the system of the embryo. The eggs may or may not be enclosed in an egg-case, which when present, is made up of only a thin diaphanous membrane.

enclosing three to five eggs, the number being subject to variation. Photo I shows the egg-case of *R. granulatus* opened to show the eggs in it. The walls of the egg-case are soft, fairly thick, highly elastic and brownish yellow in colour. The two poles of the egg-case show slight foldings, which, as the embryos grow, unfold gradually making room for the developing embroyos. The surface shows closely arranged parallel lines. Setna and Sarangadhar (1948 *a*) have described the egg-cases of *P. cuspidatus* in detail and mention that the egg-case *R. djiddensis* is exactly similar to that of *P. cuspidatus*. Microtome sections of the wall of the egg-case of *R. granulatus* show three distinct layers (Fig. 1). Mallory's triple stain colours the inner and the outer zones orange and the middle layer light blue. The outermost is the thinnest layer and is composed of horizontal striations with lacunar spaces. The narrow light blue middle layer has a beaded appearance and the innermost thick layer is composed of horizontal striations with lacunar spaces. Similar sections of the wall of the egg-cases of *P. cuspidatus* and *R. djiddensis* show the three layers described above.

Tiny protuberances are described by Nalini (1940) as occurring on the outer surface of the egg-case of *Chiloscyllium griseum*. These are not present on the egg-cases of the ovo-viviparous forms described here, the surface being smooth and even. Couch (1847) observed that the egg-case of a species of *Myliobatus* has the surface reticulated.

Nalini (1940) observed in the egg-case of *C. griseum* that the outermost layer is followed by a clear space and this has been interpreted to represent a slight pause in the secretory activity of the nidamental gland. In all the three species so far described by the author no such clear space has been noticed. If the clear space is to represent a quiescence in the secretory activity of the gland, as suggested by Nalini, then it seems that, in the species under consideration, when once the secretory activity of the gland has started there seems to be no pause until one egg-case is completed.

The maximum thinning of the egg-case has taken place in the typical viviparous forms, where the egg-case is made up of a thin diaphanous, elastic and transparent membrane which has a slight yellow or brown colour in most species.

In a specimen of *Galeocerdo tigrinus*, caught off the Madras Coast, each uterus contained twenty eggs, each enclosed in an egg-case. The egg-case of this species has already been described by Sarangadhar (1943). It is soft, thin and transparent with both ends highly folded. Between the egg and the egg-case there is a layer of albuminous fluid. The folds, as already mentioned in the case of *R. granulatus* and other ovo-viviparous species, unfold as the embroyo develops giving enough space for it. An examination of sections of the wall of the egg-case stained with Mallory's triple stain shows that it is composed of a single homogeneous compact layer as the sections are stained uniformly red. Striations and lacunar spaces which are seen in the sections of the egg-case of *R. granulatus* are not present here. In *Carcharinus dussumieri* one pole of the egg-case is continued as a long twisted cord, which is highly folded and has a golden colour. The cord measures from 220 to 250 mm. in length. The egg-cases of *Hemigaleus balfouri* resemble more or less those of *C. dussumieri* in appearance. Here too, one pole is continued into a twisted and highly folded cord measuring about 60 mm. In *Scoliodon palasorrah* there is a similar covering for the egg (Plate; photo. 2) but the long cord has been reduced to a small conical, highly folded and compressed tuft-like structure measuring about 15 to 20 mm. in length. The egg-cases of both *H. balfouri* and *S. palasorrah* have a light brown colour. The tiny egg of *S. sorrakowah* is covered over by a very delicate, transparent and colourless membrane. The egg-case (Plate; photo. 3) is pear-shaped and measures about 5 mm. by 3 mm. and it is likely that this happens to be the smallest egg-case known. The narrow part of the egg-case is drawn out into a small tuft, about 2 mm. in length when stretched out, whereas the tuft at the broad end of the egg-case is comparatively short. The egg-case is filled with a clear transparent liquid.

Microtome sections of the egg-cases of the last four viviparous species described were examined. Unlike the structure of the egg-cases of the ovo-viviparous forms, there is no differentiation into layers as revealed by the fact that the sections, when stained with Mallory's triple stain, take a uniform light red colour as in *G. tigrinus*. Lacunar spaces as well as striations are not present. All the egg-cases are composed of a single homogeneous compact layer.

The egg-cases are retained in the uteri, even in the viviparous forms, for a fairly long time and even after the young are liberated portions of the egg-case can be seen in the uteri. In certain forms like *Mustelus laevis* it has been noticed by Hoedemaker (as quoted by Mahadevan, 1940) that the membranous egg-case persists between the maternal and foetal tissues of the placenta. It permits ready diffusion of the milky nutritive fluid secreted by the uterine mucosa. According to Norman (1947) the egg-capsule formed in viviparous forms is absorbed later on.

Formation of the Elasmobranch Egg-case

There is a good deal of uncertainty still on this subject. Earlier workers like Gerbe (1872), and Perravex (1884) held that the albumen and the shell are secreted simultaneously around the egg. The latter held that although secretion of the matter, of which the shell is composed, begins before the egg reaches the gland, yet the shell is actually formed when the egg reaches the gland. But Beard (1890) stated that in skates the lower half of the purse is formed before the egg enters the oviducal gland and the closure of the purse is effected soon after the arrival of the egg. Among the more recent workers Borcéa (1904) opines that the formation of the shell commences before the egg reaches the gland on the ground that the pressure of the egg within the gland would prevent the secretion from passing between the lamellae, at the base of which individual tubular glands open. Widakowich (1905), while describing the nidamental glands of *Scyllium canicula,* held that the caudal processes of the egg-case are laid down during the passage of the egg down that part of the oviduct which is cranial to the nidamental gland, but that the body of the

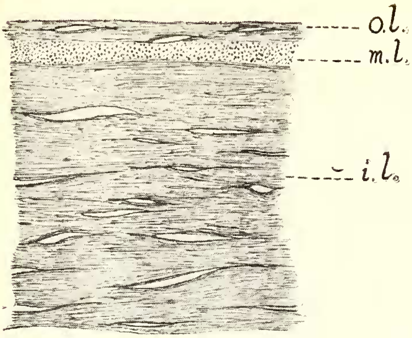

Figure 1. A section of the wall of the egg-case of *Rhinobatus granulatus*. Note the three distinct regions. × 600 (oil)

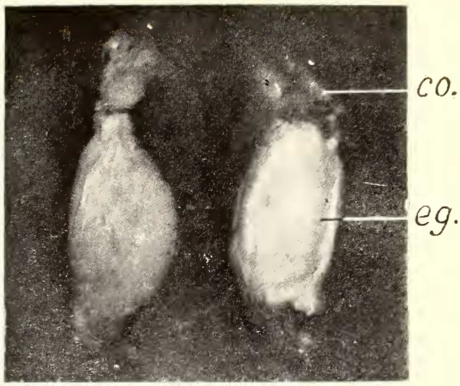

Photo 2. Egg-case of *Scoliodon palasorrah* *ca.* $\frac{2}{3}$ natural size.

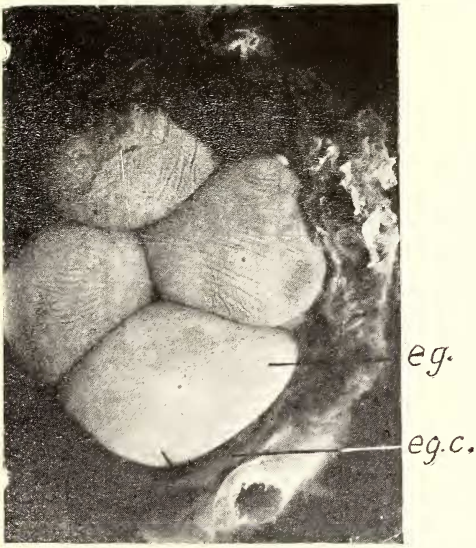

Photo 1. Egg-case of *R. granulatus* (in uterus) opened to show the eggs. *ca.* $\frac{1}{4}$ natural size.

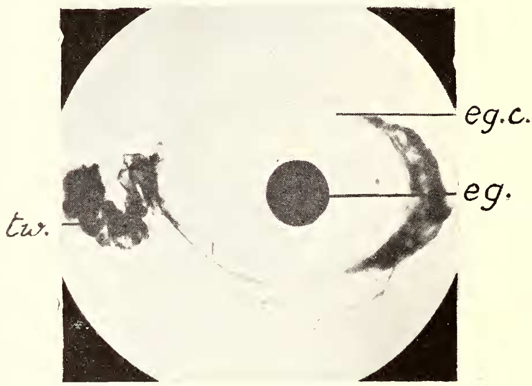

Photo 3. Egg-case of *S. sorrakowah*. Note the narrow end drawn out into a short cord. × 8

Key to Lettering

co.	....	conical tuft.
eg.	....	egg.
eg.c.	....	egg-case.
i.l.	....	inner layer.
m.l.	....	middle layer.
o.l.	....	outer layer.
tw.	....	twisted cord.

egg-case is formed during the subsequent movement of the egg through the gland. Hobson (1930), after examining about 150 pregnant skates of several species, came across a single specimen in which the egg-cases were in the process of formation. He found ova in the upper oviducts, between the ostium and the nidamental gland, whilst the egg-cases were three-quarters completed; their only difference from the final product was their light colour and soft texture. The egg-cases were quite empty and the dorsal and ventral walls were well separated from one another. On the evidence of this he concluded that the posterior three-quarters of the egg-case is secreted before the ovum enters the nidamental gland and probably half of it before the ovum has left the ovary. Garrault and Filhol (1937) have described the mechanism of secretion of the different layers of the egg-case of *Raja batis* and *Scyliorhinus canicula* but they do not mention whether the secretion of the egg-case starts before the egg reaches the nidamental gland or after that. Metten (1939) examined several specimens in order to establish the truth or otherwise of Hobson's contention. He has given a record of a number of partially secreted egg-cases. According to him there was never an ovum present in less than three-quarters completed egg-case; nor was an ovum to be found undergoing migration in the coelom or upper oviduct in any fish where the egg-cases were half secreted or less. He was not able to find any fish in the exact condition of Hobson's skate, although he found fully formed egg-cases containing only albumen. But these were rather small, otherwise normal. Nalini (1940) rejects the view of the part formation of the egg-case and concludes that the secretions are poured over the egg after it reaches the nidamental gland. She also suggests that the mode of formation of egg-case may vary in different species of oviparous Elasmobranchs. Setna and Sarangadhar (1948 *a*) observed incompletely formed egg-cases in the nidamental gland of *Chiloscyllium griseum* and remark: 'The most interesting features were, however, presented by the incompletely formed egg-cases in both the nidamental glands of the female (Text-fig. 2c; Pl. I, fig. 2 left). Both of them were equal in development, similar in orientation, which itself was similar to that of the fully formed egg-cases and they were situated exactly opposite to each other. It was obvious that nearly two-thirds of their development had been completed, characteristically, from the posterior end forwards and that anteriorly they were open, the openings being fairly wide and irregular in outline. The fertilised eggs, surrounded by dense masses of transparent, gelatinous albumen, had already entered the egg-cases, and more albumen was seen to be still entering through the open ends'. While discussing the mode of formation of the egg-case in *C. griseum* the authors remark: 'Observations on the egg-cases obtained by us point to a lack of uniformity in the composition of the structure of the capsular wall in different regions and clearly suggest a non-synchronous activity of the shell-glands in different zones of the nidamental glands. These features, together with the very incomplete nature of the egg-cases encountered by us, thus support the former view, *that the lower half or more of the egg-case is formed before the egg arrives in the nidamental gland and that the closure of the purse is effected only* *after the entry of the egg in the partially formed egg-case,*[1] regarding the formation of the egg-case in oviparous forms.'

The above-mentioned observations have all been restricted to oviparous forms. The condition of the egg-case in the ovo-viviparous forms such as *Rhinobatus granulatus*, *Rhynchobatus djiddensis* and *Pristis cuspidatus* suggest the improbability of the egg-case being formed after the egg reaches the nidamental gland. The mode of formation of the egg-case, which the author believes to be of general occurrence in Elasmobranchs, would seem applicable to all forms. In all the ovo-viviparous species described, a single egg-case covers more than one egg. Usually the number varies from three to five. This arrangement stood against the acceptance of the view that the egg-case is being secreted around the egg or eggs after they reach the nidamental gland. If, according to Borcéa (1904), one egg in the nidamental gland can give so much pressure as to prevent the secretions from flowing out, what will be the pressure exerted on the gland by three to five large ova each measuring about 50 mm. in diameter?

Most of the previous workers agree that the formation of the shell commences before the egg reaches the gland. It has been doubted whether normal egg-cases can be formed, considering the highly sticky nature of the secretions, when there is no egg in the nidamental gland to keep its walls separate and to prevent the walls of the egg-case from collapsing (Nalini, 1940). The observations of Beard (1890) show that about ten per cent of some shark egg-cases laid in captivity were found to contain no egg. More instances of such egg-cases, containing no egg, have been recorded by Borcéa (1904), Metten (1939), Gudger (1940) and Smith (1942). These records substantiate the fact that the walls of the egg-case can remain separate even though there is no egg in between. Further, it is not unlikely that a certain quantity of albumen will be secreted into the egg-case that is in the process of formation and this will keep the walls from collapsing. As Metten (1940) has remarked some egg-cases, even though they do not contain the eggs, have albumen inside. Externally, these 'empty egg-cases, it is reported, are quite indistinguishable from others, except for their lighter weight. Such empty egg-cases are sometimes known as 'wind eggs'.

In a mature female specimen of *Galeocerdo tigrinus*, caught off the Madras Coast on August 10, 1944 measuring 3775 mm. in length, two eggs, one in each cranial oviduct, were seen migrating down into the nidamental glands. They had already travelled about one-third of the distance from the oviducal funnel to the nidamental gland. An examination of these glands revealed that they had already begun to secrete the egg-case and part of the egg-case formed could be traced from the lateral horns of the gland to the caudal oviduct. The portion that had already been formed would evidently constitute the highly compressed and twisted cord at one pole of the egg-case. The very fact that one seldom encounters a partly formed egg-case as the one mentioned here, suggests that the formation of the egg-case is rather quick and hence it is only by pure chance that one

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[1] Note: Italics by author.

may come across a specimen with an incomplete egg-case in the nidamental gland and as Setna and Sarangadhar (1948 *a*) have pointed out a more intensive fishing during the breeding season may reveal the normality of the phenomenon of part formation of egg-cases.

In those forms where more than one egg is enclosed by an egg-case the theory of egg-case formation *en masse* does not seem to be applicable because all eggs which are to be enclosed by an egg-case cannot reach the nidamental gland simultaneously; even if they reach the gland in quick succession the glands will have to remain inactive until all the eggs reach the gland. So taking these facts into consideration the following conclusions may be drawn. The nidamental gland begins to secrete the egg-case as soon as ovulation takes place, whether ovulation be the only stimulus or not, and consequently when the egg reaches the nidamental gland there will be a partly formed egg-case to receive the egg. Fresh secretions, being in the form of granules and fibres, are dovetailed so closely as not to leave any definite suture. Further, it is important to emphasise that when once the secretory phase of the gland has started it stops only after the completion of an egg-case and thus the formation of the egg-case is a continuous process which eliminates the possibility of the presence of a suture denoting the line of fusion.

Summary

1. Egg-cases of three ovo-viviparous forms viz., *Rhinobatus granulatus, Rhynchobatus djiddensis* and *Pristis cuspidatus* and five viviparous species viz., *Galeocerdo tigrinus, Carcharinus dussumieri, Hemigaleus balfouri, Scoliodon palasorrah* and *S. sorrakowah* have been described.

2. The egg-cases of oviparous species are thick and horny exhibiting distinct layers, while viviparous forms have thin and transparent egg-cases of a homogeneous substance not marked into distinct layers. In ovo-viviparous species the egg-cases formed are intermediate in their structure and thickness.

3. The probable mode of formation of the egg-case together with the stage at which secretion begins is suggested.

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